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RESEARCH ARTICLE

How does forest fragmentation affect tree communities? A critical case study in the biodiversity hotspot of New Caledonia

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Abstract
Context The biodiversity hotspot for conservation of New Caledonia has facing high levels of forest fragmentation. Remnant forests are critical for biodiversity conservation and can help in understanding how does forest fragmentation affect tree communities.
Objective Determine the effect of habitat configuration and availability on tree communities.
Methods We mapped forest in a 60 km^2 landscape and sampled 93 tree communities in 52 forest fragments following stratified random sampling. At each sampling point, we inventoried all trees with a diameter at breast height $\geq$10 cm within a radius of 10 m. We then analysed the response of the composition, the structure and the richness of tree communities to the fragment size and isolation, distance from the edge, as well as the topographical position.
Results Our results showed that the distance from the forest edge was the variable that explained the greatest observed variance in tree assemblages. We observed a decrease in the abundance and richness of animal-dispersed trees as well as a decrease in the abundance of large trees with increasing proximity to forest edges. Near forest edges we found a shift in species composition with a dominance of stress-tolerant pioneer species.
Conclusions Edge-effects are likely to be the main processes that affect remnant forest tree communities after about a century of forest fragmentation. It results in retrogressive successions at the edges leading to a dominance of stress-tolerant species. The vegetation surrounding fragments should be protected to promote the long process of forest extension and subsequently reduce edge-effects.

Keywords Dispersal mode · Edge-effect · Fragment size · Landscape · Habitat loss · Topographic position

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Introduction

Habitat loss decreases the amount of habitat, but it also changes its configuration through fragmentation, i.e. the process during which “a large expanse of habitat is transformed into a number of smaller patches of smaller area, isolated from each other by a matrix of

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habitats unlike the original" (Wilcove et al. 1986). Today, forest fragmentation has reached such proportions that much of the Earth's remaining fragments are less than 10 ha in size and 70% of remaining forest is within 1 km of a forest edge (Haddad et al. 2015). Recently, Brinck et al. (2017) showed that 19% of the remaining area of tropical forest is within 100 m of a forest edge and that edge effects account for 31% of the currently estimated annual carbon releases due to tropical deforestation. In this context, understanding the effects of fragmentation on the composition, the richness and the structure of communities is a critical issue for biodiversity conservation planning (see Wilson et al. 2016).

Forest fragmentation has been identified for a long time as one of the main causes of biodiversity loss (Turner 1996). However, the relative importance of the effects of habitat loss and the effects of fragmentation per se, i.e. independently of the effect of habitat loss (hereafter fragmentation), is still a subject of debate (see Fahrig 2003, 2013; Didham et al. 2012). One of the basic potential effects of fragmentation is that a decrease in fragment size, an increase in fragment isolation, or both, lead to fragments with fewer species due to both increasing extinction and decreasing immigration rates (MacArthur and Wilson 1967). It is expected that the higher the level of fragmentation is, the greater will be the decrease in species richness and the longer the life-span of species is, the more time it will take for that decrease to be seen (Kuussaari et al. 2009).

In addition to habitat loss, one of the most obvious changes to a fragmented landscape is the creation of new edges. These new edges result in many abiotic (e.g. increase in air temperature, vapour deficit pressure, light availability and wind disturbances) and biotic edge-effects (e.g. modification of seed dispersal) which greatly and deeply change the composition and the structure of communities (Murcia 1995; Harper et al. 2005). In their overview, Harper et al. (2005) showed that the creation of new forest edges is expected to increase tree mortality by 50% within the first 100 m, which modifies forest structure (e.g. decrease in canopy cover), which in turn modifies the structure (e.g. higher stem density) and composition (e.g. increase in exotic and shade-intolerant species) of communities.

The drivers and the strength of plant community changes will depend on the size, the shape and the distribution of fragments in the landscape, as well as the total amount of habitat and the nature of the non-habitat matrix (see Fahrig 2003; Ewers and Didham 2006; Laurance 2008). For instance, both the magnitude of edge influence (i.e. the extent to which plant community differs at the edge) and the depth or distance of edge influence (i.e. the distance from the edge over which there are significant differences) increase with increasing contrast between forest fragments and the surrounding vegetation, and the area influenced by edges increases with both decreasing fragment size and compactness (Harper et al. 2005). In parallel, species respond differently to fragmentation according to the size of their populations as well as their functional attributes. For instance, fragmentation induces edge-effects that increase the mortality of late successional species and provide good environmental conditions for the proliferation of stress-tolerant pioneer species (e.g. Laurance et al. 2006; Lôbo et al. 2011; Orihuela et al. 2015). Likewise, in small isolated fragments, communities and seed rains mainly consist in small-seeded wind-dispersed species, while in large and less isolated fragments they mainly consist of large-seeded animal-dispersed species (e.g. Metzger 2000; Jesus et al. 2012; Mendes et al. 2016).

Forest fragmentation is usually a non-random process and the configuration of remaining forest fragments often reflects environmental factors, such as topography, soil type or wetness (Turner 1989; Laurance 2008). For instance, in agricultural landscapes, forest is preferentially cleared on flat, rich and well-drained soils, while in fire prone landscapes, forest is mostly burnt on dry, wind-exposed slopes and ridges. Soil type, along with nutrient and water availability or wind exposure, are also related to topography (e.g. ridges are more nutrient-poor, drier, and more exposed to wind than slopes or gorges). Topography can therefore influence the processes shaping forest structure and composition, and ignoring this influence runs the risk of misinterpreting fragmentation effects (Dorner et al. 2002).

In the biodiversity hotspot of New Caledonia (Mittermeier et al. 2004), more than 75% of forest cover has already been destroyed and forests are now very fragmented, especially at low and middle elevation (Jaffré et al. 1998). New Caledonian landscapes on ultramafic substrates are critical places for biodiversity conservation and are a suitable place to study the consequences of fragmentation for forest biodiversity. Forests on these substrates harbour an outstanding flora but have seen high deforestation rates due to logging, mining and bushfires. Today they only cover about 1100 km^2 (Jaffré et al. 2009; Jaffré and L'Huillier 2010b) and mainly consist of scarce remnant fragments scattered in a matrix of shrubby vegetation called "maquis" (McCoy et al. 1999). Furthermore, edges and contrasts between these fairly different vegetation types are often sharpened by fire (Curt et al. 2015).

Here, we analysed the effects of the forest fragment size, isolation and proximity to edges on the composition, the structure and the species richness of tree communities. We also tested whether or not these effects differed depending on the topographic position of tree communities. Given the high contrasts between forests and the surrounding vegetation as well as the high level of fragmentation, we expect that edges result in major changes in the structure, composition and richness of tree communities, and that this occurs deeply into the forest. We also expect that the species richness of tree communities decreases with decreasing fragment size, increasing isolation or both.

Methods

Study area

New Caledonia is an archipelago with a land area of about 18,500 km^2 located slightly north of the Tropic of Capricorn (20–23°S, 164–167°E), about 1500 km east of Australia and 2000 km north of New Zealand. One of the most outstanding features of the New Caledonian flora is inherent to the presence of ultramafic substrates (also known as serpentine soils, see Proctor et al. 1988) that cover about one-third (5600 km^2) of the main island area (Grande Terre, 16,500 km^2) but less than 1% of the Earth's land area (Brooks 1987). These substrates are stressful for plants due to low levels of macronutrients and high levels of potentially phytotoxic metals such as nickel, and to a low water-holding capacity (Brooks 1987; Proctor et al. 1988). Plant communities on such substrates therefore typically display poor productivity (Kazakou et al. 2008). As a result, the process of secondary succession to rebuild forest is particularly long (in New Caledonia more than 200 years according to Perry and Enright 2002). In New Caledonia, ultramafic substrates harbour 2145 vascular plant species on only 5600 km^2 (Jaffré et al. 2009; Morat et al. 2012; Isnard et al. 2016). More than half of these species are endemic to New Caledonian ultramafic substrates, which constitutes the world's richest endemic ultramafic flora.

Anthropogenic forest fragmentation is relatively recent. It started with Melanesian settlement about 3000 years ago before it sharply increased with Western settlement at the end of the eighteenth century (see Richer de Forges and Pascal 2008). In the Grand Massif du Sud the main causes of forest fragmentation have been logging, mining activities and bush fires. Logging started in the mid-nineteenth century while nickel mining started later at the end of the nineteenth century and caused a dramatic increase in forest fragmentation due to extensive prospection during which vegetation was burned to access outcrops. Today, logging is negligible while mining is booming (see L'Huillier and Jaffré 2010) and has emerged as the main threat to New Caledonian biodiversity (Pascal et al. 2008).

The study site was located in the southern part of the New Caledonian main island near Plaine des Lacs in the Grand Massif du Sud (Fig. 1a). It was also located near one of the largest nickel-mining extraction sites in New Caledonia. The studied landscape was about 60 km^2 (10 × 6 km), located between 200–600 m in elevation and received 2500–3000 mm/year rainfall. Forest fragments covered about 5.5% of the landscape and were distributed in a matrix of vegetation that ranged from open low maquis (ligno-herbaceous sclerophyllous shrublands) to continuous tall maquis dominated by *Gymnostoma deplancheanum* (see McCoy et al. 1999; van der Ent et al. 2015). The pedology associated with ultramafic substrates is quite complex because of the different levels of alteration of the bedrock (Jaffré 1980). Here, we considered three broad soil types in relation with topography (Jaffré and L'Huillier 2010a): eroded and often shallow ferralsols on the hills (partially covered by screes and colluvium), deep ferralsols modified by colluviation on foothills, and ferralsols on alluvium and colluvium in the plain. In the last case, soils are often hydromorphic and forest actually grows on sparsely distributed gravelly or Planthic non-hydromorphic ferralsols.

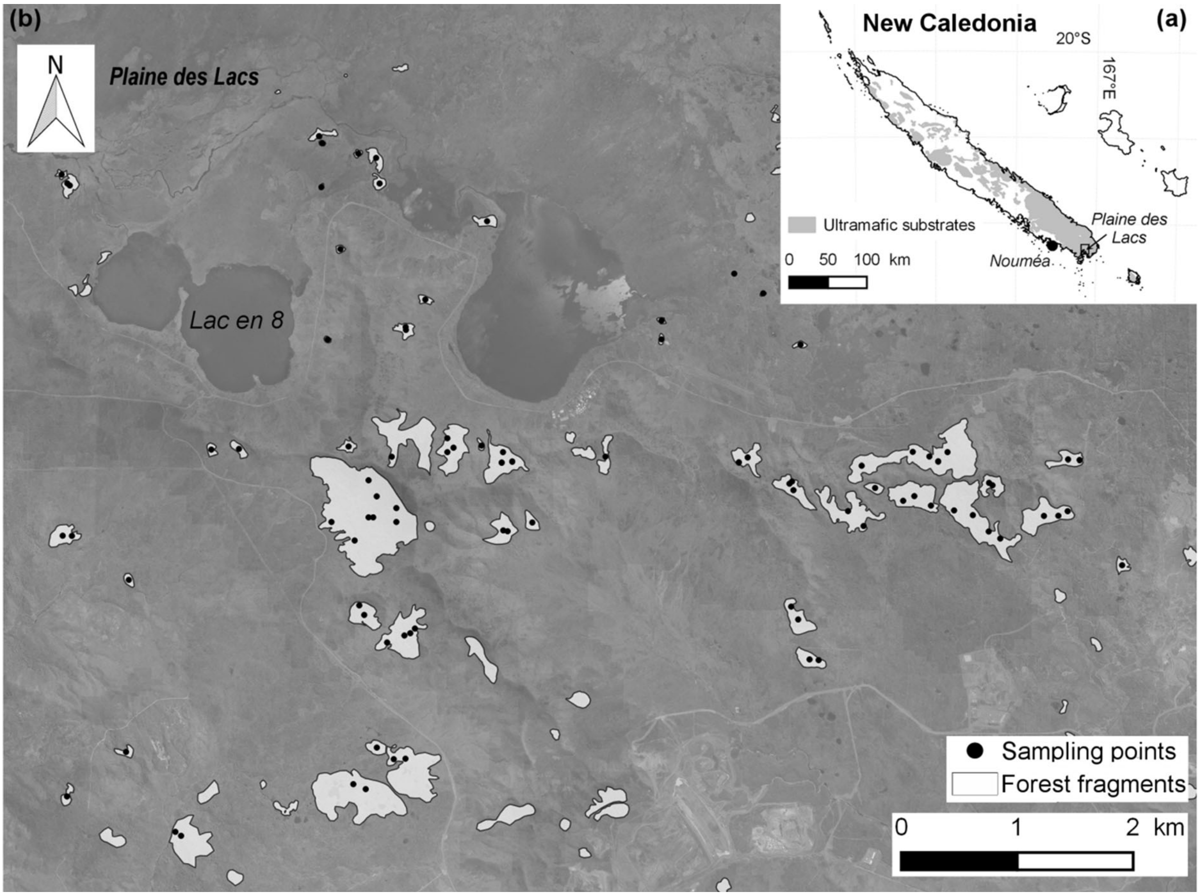


Fig. 1 Location of **a** the studied landscape in southern New Caledonia near Plaine des Lacs (freshwater reserve designated as a RAMSAR site) and **b** the 93 sampling points across forest fragments

Sampling scheme

We carried out stratified random sampling of tree communities. All forest fragments within the study area were manually delineated on a 1:3000 scale from recent aerial photographs available online (www.georep.nc). Of the 95 forest fragments we delineated, we ultimately sampled 52 accessible fragments with a size ranging from 0.1 to 54.6 ha (median 1.6 ha). These forest fragments were sampled randomly and proportionally to their sizes. This sampling scheme was used in order to explore how the distance from the forest edge and topographical position affected tree communities in large fragments. We first applied a 20 × 20-m regular grid on the study area and a 10-m buffer on each forest fragment to exclude edges. We then sampled the centroid of each fragment plus additional points randomly selected on the grid as a function of fragment size. The number of sampling points varied from 1 for small forest fragments (<3 ha) to 8 for the largest fragment (54.6 ha) for a total of 93 tree communities sampled. At each sampling point, we inventoried all trees with a diameter at breast height (i.e. at 1.3 m, DBH) ≥10 cm within a radius of 10 m (i.e. in an area of 314 m^2). Most species were identified in the field, but in cases where identity was in doubt, samples were collected and identified by comparison with the collection voucher specimens in the IRD herbarium in Nouméa (NOU). Plant names follow FLORICAL nomenclature (Morat et al. 2012).

Dispersal mode

We explored whether tree species responded differently to forest fragmentation depending on their expected dispersal modes. We classified the seed dispersal mode of each inventoried tree species as dispersed by animals, wind or gravity. Dispersal modes were either extracted from Carpenter et al. (2003), or determined according to fruit and seed morphology. Species with fleshy fruits, arils or other edible appendages were considered as dispersed by animals (i.e. mainly birds and bats in New Caledonia, see Carpenter et al. 2003). Species with dry fruits and particular seed appendages such as wings or hairs were considered as dispersed by wind, while species without particular appendages were considered as dispersed by gravity. Fruit and seed morphology were either checked in the field or with voucher specimens at the herbarium in Nouméa (NOU). When available, dispersal modes were also checked in the literature (Aubréville et al. 1967-present).

Data analyses

All statistical analysis were conducted with R (2.15.2, R Core Team 2012). For each sampling point, we extracted the following features: the fragment size, fragment isolation (computed as the edge-to-edge distance from the nearest forest fragment), the distance from the nearest forest edge and the topographical position. These variables were log-transformed before performing the following analyses. Topographical positions in relation to soil types (i.e. shallow ferralsols on the hills, deep ferralsols on foothills and ferralsols on alluvium and colluvium in the plain) were extracted from a 1:50,000 scale geological map of New Caledonia (from DIMENC/SGNC-BRGM and downloaded on Géorep, http://www.geoportal.gouv.nc).

We first analysed the variability in floristic composition at fragment level ($N = 56$). To do this for each fragment, we only considered the sampled tree community located farthest from the forest edge. We then performed an ordination by non-metric multidimensional scaling (NMDS) to graphically analyse variation in tree species composition across the sampling points. We used Bray-Curtis distances computed on species abundances as a floristic dissimilarity index. NMDS was performed using the metaMDS function from the vegan R package (Oksanen et al. 2013) which finds the most stable NMDS solution (i.e. which minimizes stress) using random reiteration (set here to a maximum of 1000 reiterations). We used a permutational multivariate analysis of variance to test the effects of fragment size, fragment isolation, distance from the nearest forest edge and the topographical position on Bray-Curtis dissimilarities (PERMANOVA, adonis function with 999 permutations). We also used the envfit function to fit sampling point features in the ordinations. This function also uses permutation tests to assess the significance of the results.

We then analysed the effect of fragment size, fragment isolation, proximity to the forest edge and topographical position on the functional composition (i.e. dispersal modes), richness and structure of tree communities using multivariate generalized linear mixed models (glmer function from the lme4 R package, Bates et al. 2015). Each fragment was added as a random effect, as in large fragments several tree communities were sampled (Bolker et al. 2009). The analysed response variables were the abundance and richness of trees, wind-dispersed trees and animal-dispersed trees. We also analysed the response of the size structure of communities by computing the mean size of the trees (as the quadratic mean DBH) as well as the number of trees in five size classes: <15 cm DBH, 15 cm $\leq$ DBH < 20 cm, DBH $\geq$ 20, 30 and 40 cm (15 cm and 20 cm being the median and third quartile of the DBH of all trees pooled together). For each response variable, we selected the best combination of predictors using the dredge function from the MuMin R package (Bartoń 2016). The best model was defined as the combination of predictors that produced the lowest corrected Akaike Information Criterion (AICc), i.e. which showed the best trade-off between the goodness of fit (likelihood) and the number of parameters. The goodness of fit of the best models with and without random effects was expressed using conditional and marginal R^2 (Nakagawa and Schielzeth 2013). The residuals of all models were normally distributed, homoscedastic and were spatially independent (tested with Moran's correlograms).

Results

In all, 3681 trees belonging to 199 species, 117 genera and 58 families were inventoried in the 93 sampled communities (see Table S1 supplementary material). On a landscape scale, the abundance of species showed very asymmetric distribution typical of tropical forests (Fig. 2a). The three most abundant species were *Codia discolor* (264 trees), *Gymnostoma deplancheanum* (223 trees) and *Arillastrum gummiferum* (198 trees) accounting for almost 20% of all

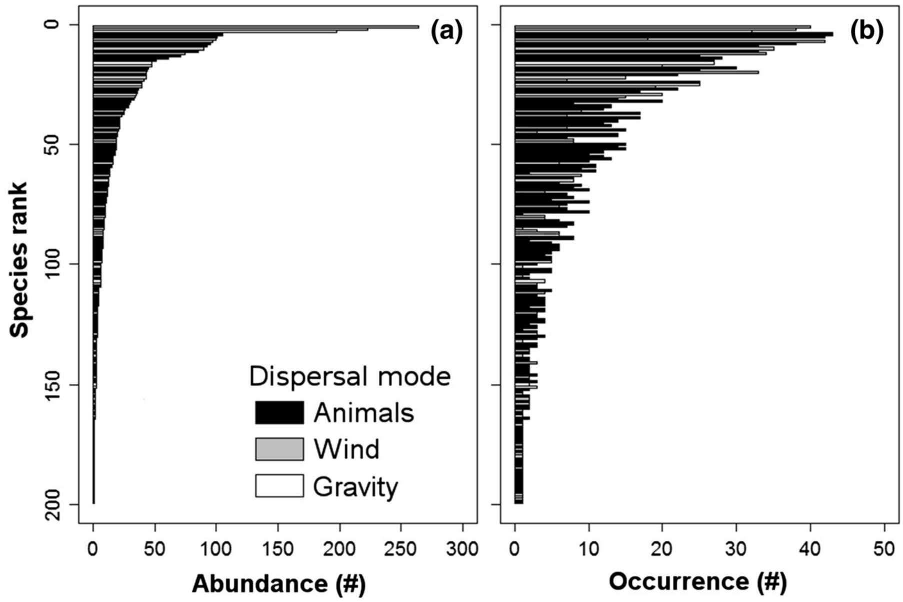


Fig. 2 Species rank abundance **a** and frequency **b** of the 199 inventoried tree species in the forest fragments

inventoried trees (Table 1). Overall, although the frequency distributions were less asymmetric, the most abundant species were also the most frequent (Fig. 2b, Spearman's rank correlation test, $\rho = 0.94$, P value < 0.001). Most of the inventoried species were dispersed by animals (69%), almost a quarter by wind (23%) and a few by gravity (8%). However, in terms of tree abundance, the dominance of animal-dispersed species was lower (52%) while wind-dispersed species accounted for more than a third of the inventoried trees (36%). Neither the abundances of species, nor their frequencies differed significantly according to their dispersal modes (pairwise Wilcoxon rank sum test, P values > 0.05).

Floristic dissimilarity between fragments was high with a Bray-Curtis index ranging from 0.27 to 1 (0.86 on average, 0.11 SD), and was not correlated with the geographical distances between sampling points (Mantel statistic based on Spearman's rank correlation, $\rho = 0.05$, P value $= 0.113$). The NMDS ordination drew a continuum between sampled tree communities rather than clearly distinct floristic groups (Fig. 3a). It should be noted that the distance from the forest edge and the fragment size were positively correlated, with communities sampled far from the edge being sampled in large fragments (Fig. 3b, Pearson's $r = 0.80$, P value < 0.001). The distance from the forest edge and the topographical position explained 6.4% and 9.1% of the variance in floristic composition (PERMANOVA, P value < 0.001) while the effect of fragment isolation was not significant (P value $= 1.166$). The left part of the first axis of the NMDS gathers tree communities sampled near forest edges in small forest fragments (Fig. 3b). These communities were mostly sampled in the plain or on the foothills and were dominated by wind-dispersed species, such as *Gymnostoma deplancheanum* or *Codia spatulata* (Fig. 3c). Conversely, the right part of the first axis of the NMDS tended to gather communities sampled further from forest edges in larger forest fragments. These communities were mostly sampled on the hills or on the foothills and were dominated by animal-dispersed species, such as *Guettarda eximia* or *Pycnandra fastuosa*.

The distance from the forest edge and the topographical position had significant effects on the composition, the richness and the structure of tree communities, but we did not find any significant effect for either the size or the isolation of the fragments (Table 2). Tree species richness increased significantly with increasing distance from the forest edge

Table 1 The 18 species accounting for 50% off all the inventoried trees

Species	Family	Abundance	Occurrence	Disperser
Codia discolor	Cunoniaceae	264	40	Wind
Gymnostoma deplancheanum	Casuarinaceae	223	38	Wind
Arillastrum gummiferum	Myrtaceae	198	32	Gravity
Plerandra gordonii	Araliaceae	105	43	Animals
Gastrolepis austrocaledonica	Stemonuraceae	101	42	Animals
Codia spatulata	Cunoniaceae	100	18	Wind
Deplanchea speciosa	Bignoniaceae	97	42	Wind
Garcinia balansae	Clusiaceae	95	38	Animals
Styphelia cymbulae	Ericaceae	93	33	Animals
Myodocarpus fraxinifolius	Araliaceae	90	35	Wind
Calophyllum caledonicum	Calophyllaceae	85	33	Animals
Flindersia fournieri	Rutaceae	75	34	Wind
Pycnandra fastuosa	Sapotaceae	71	25	Animals
Apodytes clusiifolia	Icacinaceae	61	28	Animals
Guettarda eximia	Rubiaceae	51	27	Animals
Neoguillauminia cleopatra	Euphorbiaceae	48	20	Gravity
Pleurocalyptus pancheri	Myrtaceae	48	27	Gravity
Alphitonia neocaledonica	Rhamnaceae	45	30	Animals

(Fig. 4b), while the relationship between the number of trees and the distance from the forest edge was significant but weak (Fig. 4a). Our best model predicted that species richness was expected to be about twice as high in the forest interior compared to near the forest edge. This increase in species richness was due to a significant increase in the abundance and richness of animal-dispersed trees (Fig. 4c, d), while the distance from the forest edge did not have a significant effect on wind-dispersed trees (Table 2). On the whole, the proportion of wind-dispersed trees and species tended to increase from the forest interiors to the forest edges with a sharper increase in the first 25–30 m from the edges (Fig. 5). Obviously, the reverse pattern was observed for animal-dispersed species, resulting in a shift in species composition.

Concerning the structure of tree communities, both the mean size of the trees and the number of large trees ($\geq$20 cm) significantly increased with increasing distance from the forest edge (Table 2; Fig. 6). Conversely, the distance from the forest edge had no significant effect on the number of smaller trees (Fig. 6b and 6c). Lastly, it should be noted that larger trees ($\geq$30 or 40 cm) tended to increase from the plain to the hills (Fig. 6e, f).

Discussion

Edge-effects on tree communities

Our results support the hypothesis that edge-effects are the main driver of changes in the composition, structure and richness of communities in fragmented landscapes (Ewers et al. 2007; Fletcher et al. 2007; Banks-Leite et al. 2010; Benchimol and Peres 2015). The most dramatic change we observed was a shift in functional composition near forest edges (i.e. in the first 25–30 m), with tree communities being dominated by pioneer wind- (or gravity-) dispersed species. This decrease (or increase) in the abundance and richness of species dispersed by animals (or other dispersers) was also reported in Brazil (e.g. Santos et al. 2008; Magnago et al. 2014). In our study, these dominant species on the edges were stress-tolerant pioneer species that often relied on frequent fires to maintain their dominance, e.g. *Codia* spp. (Ibanez and Birnbaum 2014), *Gymnostoma deplancheanum* (McCoy et al. 1999) or *Arillastrum gummiferum* (Demenois et al. 2017), which highlights the importance of synergistic effects of fragmentation, drought and fire in shaping tree communities (e.g. Brando et al. 2014; Alencar et al. 2015).

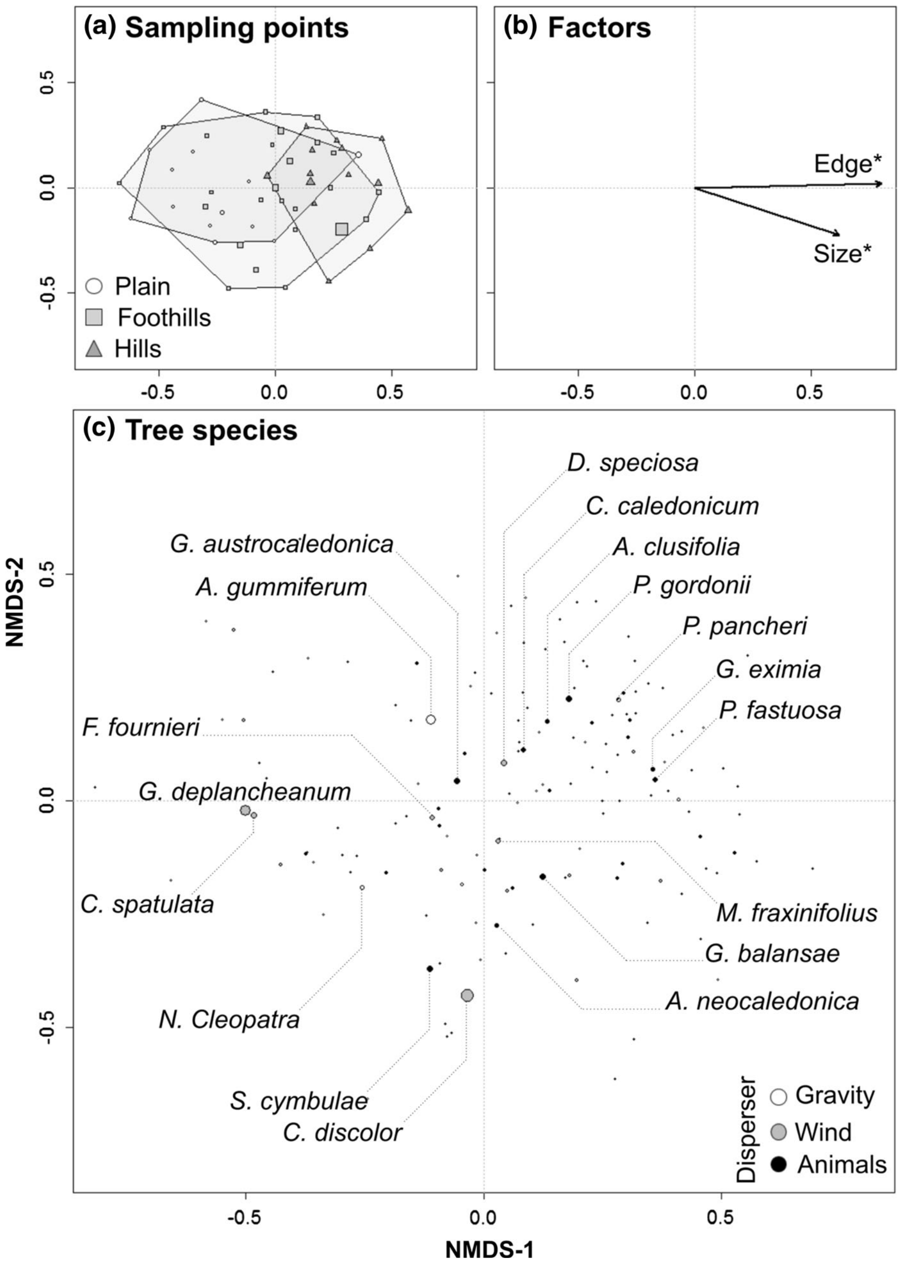


Fig. 3 Non-metric multidimensional scaling (NDMS) ordination of fragments (**a**), environmental factors (**b**) and tree species (**c**) using Bray-Curtis distances on species abundances (stress = 0.24). Only significant factors are represented ('*' *P* value < 0.05, '**' *P* value < 0.01, '***' *P* value < 0.001) and the length of arrows is proportional to the goodness of fit (R^2) with the ordination (**b**). Point size is proportional to the distance from the forest edge in **a** and to species abundance in **c**

The proliferation of pioneer species in fragmented landscapes is also usual in Brazil and is very likely to occur quite rapidly (only a couple of decades) after forest fragmentation owing to a rapid increase in late successional species mortality caused by exposure to wind, drought and fire, as well as a possible increase in the seed rain from pioneer species (see Laurance et al. 2006; Benchimol and Peres 2015). Laurance et al. (2000) also showed that the mortality of large trees is also disproportionately greater near forest edges (<300 m from the edge) in comparison with the forest interior (>300 m from the edge) and smaller trees because large trees are more vulnerable to wind disturbance and drought stress which are greater near the forest edge. Along these lines, and as reported in Brazil (Oliveira et al. 2008; Santos et al. 2008), we

Table 2 Top generalized linear mixed models ($\Delta AIC_c < 2$) predicting the richness, composition and structure of tree communities

Response variables[a]	Range	Model rank	AIC_c	R^2_m	R^2_c	Intercept	Parameter (±SD)			
							Fragment size	Fragment isolation	Distance from the edge	Topographical position
Number of species	5–33	1	610.686	0.201	0.581	1.861 ± 0.230***			0.236 ± 0.059***	Plain −0.064 ± 0.113 Hills 0.189 ± 0.075
		2	611.536	0.241	0.611	1.974 ± 0.224***	0.047 ± 0.040		0.236 ± 0.059**	Plain −0.052 ± 0.052 Hills −0.078 ± 0.074
		3	612.391	0.209	0.581	2.018 ± 0.263***		−0.024 ± 0.032	0.230 ± 0.060***	Plain −0.034 ± 0.053 Hills −0.120 ± 0.073
Number of animal-dispersed species	0–26	1	573.912	0.218	0.718	0.920 ± 0.308***			0.340 ± 0.078***	Plain −0.056 ± 0.160 Hills 0.354 ± 0.100
		2	575.628	0.246	0.735	1.065 ± 0.295***	0.044 ± 0.058		0.318 ± 0.083***	Plain −0.108 ± 0.072 Hills −0.132 ± 0.105
		3	575.904	0.222	0.720	1.137 ± 0.360**		0.026 ± 0.048	0.335 ± 0.079***	Plain −0.092 ± 0.072 Hills −0.169 ± 0.104
Number of trees	15–63	1	716.231	0.054	0.284	3.219 ± 0.145***			0.114 ± 0.039 **	
		2	717.347	0.076	0.296	3.265 ± 0.151***	0.026 ± 0.025		0.095 ± 0.043 *	
Number of animal-dispersed trees	0–54	1	734.832	0.220	0.649	1.463 ± 0.241***			0.373 ± 0.064***	Plain 0.003 ± 0.065 Hills −0.224 ± 0.097*
		2	736.082	0.246	0.667	1.481 ± 0.243***	0.063 ± 0.062		0.355 ± 0.066***	Plain −0.008 ± 0.065 Hills −0.196 ± 0.100*

Table 2 continued

Response variables[a]	Range	Model rank	AIC_c	R^2_m	R^2_c	Intercept	Parameter (±SD)			
							Fragment size	Fragment isolation	Distance from the edge	Topographical position
Quadratic mean DBH	9–37	1	557.807	0.207	0.437	7.344 ± 3.182			3.727 ± 0.879	Plain −1.442 ± 0.709 Hills 0.475 ± 0.910
		2	559.734	0.207	0.442	7.499 ± 3.504	0.065 ± 0.488		3.668 ± 1.025	Plain −1.455 ± 0.724 Hills 0.524 ± 0.970
Number of trees DBH < 15 cm	3–36	1	679.757	0.043	0.043	2.962 ± 0.041***				Plain 0.114 ± 0.043** Hills −0.119 ± 0.059*
		2	681.636	0.044	0.044	2.949 ± 0.047***	0.017 ± 0.028			Plain 0.107 ± 0.045* Hills −0.106 ± 0.063
Number of trees 15 cm ≤ DBH <20 cm	1–22	1	503.309	0.000	0.156	2.108 ± 0.049***				
		2	504.358	0.016	0.149	2.076 ± 0.058***	0.031 ± 0.031			
		3	505.210	0.003	0.155	2.163 ± 0.123***		−0.014 ± 0.029		
		4	505.298	0.003	0.151	2.010 ± 0.257***			0.027 ± 0.070	
Number of trees DBH ≥20 cm	0–22	1	547.463	0.147	0.516	0.998 ± 0.289***			0.334 ± 0.078***	
		2	547.936	0.169	0.511	1.241 ± 0.339***		−0.052 ± 0.040	0.323 ± 0.078***	
		3	549.005	0.177	0.538	0.900 ± 0.298**			0.367 ± 0.081***	Plain −0.113 ± 0.068 Hills 0.077 ± 0.089
		4	549.221	0.165	0.534	1.054 ± 0.303***	0.032 ± 0.049		0.310 ± 0.086***	
Number of trees DBH ≥ 30 cm	0–10	1	411.509	0.210	0.371	−0.576 ± 0.468			0.451 ± 0.124***	Plain −0.034 ± 0.101 Hills −0.220 ± 0.137
		2	413.203	0.142	0.359	−0.616 ± 0.003***			0.466 ± 0.003***	
		3	413.357	0.224	0.394	−0.475 ± 0.494		0.047 ± 0.071	0.410 ± 0.139**	Plain −0.045 ± 0.103

Table 2 continued

Response variables[a]	Range	Model rank	AIC_c	R^2_m	R^2_c	Intercept	Parameter (±SD)			
							Fragment size	Fragment isolation	Distance from the edge	Topographical position
Number of trees DBH ≥ 40 cm	0–6	1	296.134	0.327	0.470	−1.827 ± 0.701**			0.524 ± 0.181**	Hills −0.193 ± 0.143 Plain 0.088 ± 0.161 Hills −0.708 ± 0.241**
		2	297.932	0.331	0.462	−1.556 ± 0.786*		−0.050 ± 0.071	0.502 ± 0.183**	Plain 0.110 ± 0.163 Hills −0.746 ± 0.245**
		3	298.059	0.341	0.489	−1.710 ± 0.731*	0.060 ± 0.101		0.472 ± 0.200*	Plain 0.077 ± 0.163 Hills −0.679 ± 0.247**

The marginal R^2 (R^2_m) describes the proportion of variance explained by the fixed predictors alone and the conditional R^2 (R^2_c) describes the proportion of variance explained by both the fixed and random predictors

'***' P value < 0.001, '**' P value < 0.01, '*' P value < 0.05, '.' P value < 0.1

[a] All models were fitted using a Poisson distribution for count data (with a log link function). Only the variance of the quadratic mean DBH was analysed using a Gaussian distribution

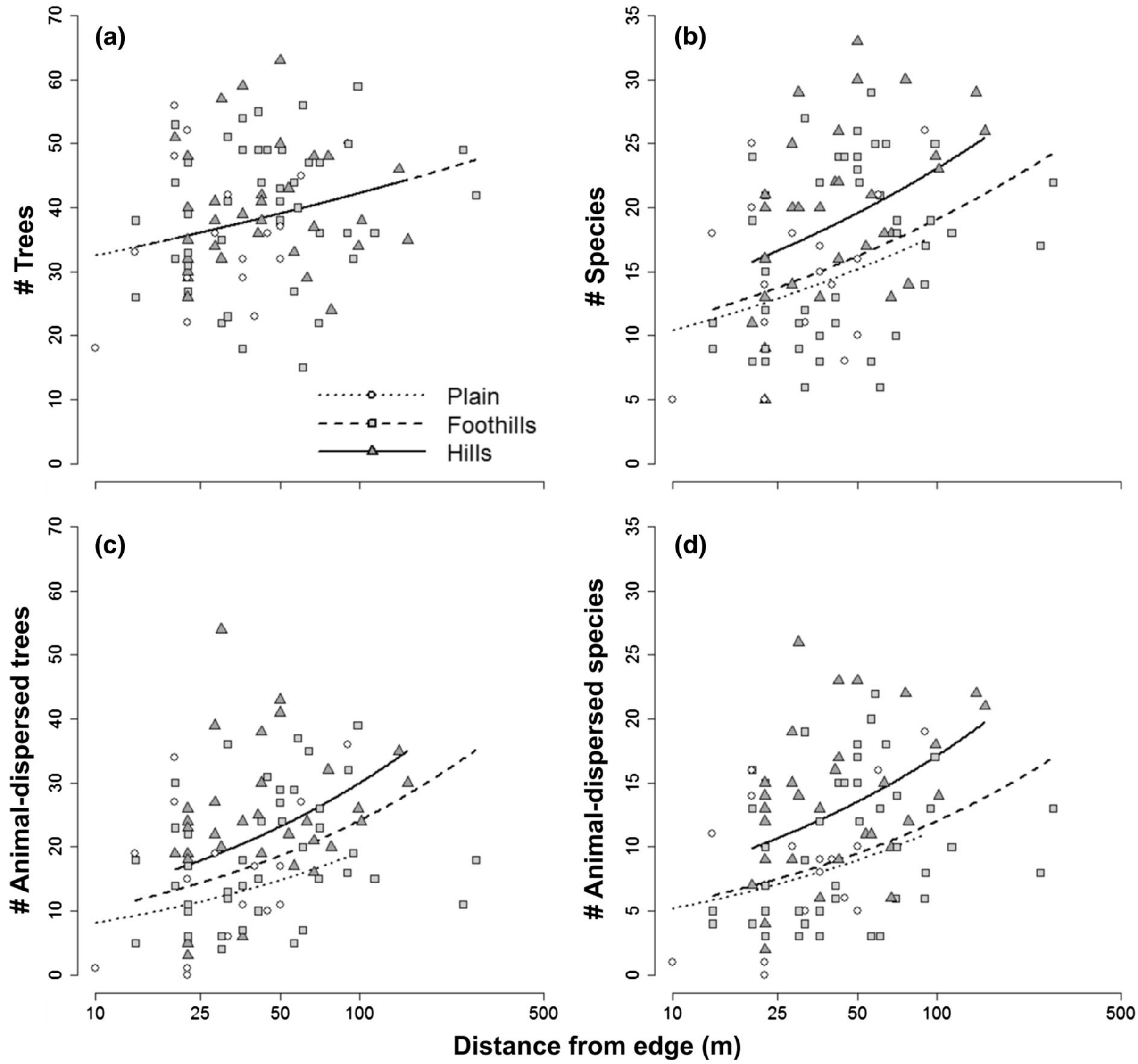


Fig. 4 Best models for the effect of the log-distance from the forest edge and the topographical position on the number of trees (**a**–**c**) and the number of species (**b**–**d**). See Table 2 for the coefficients and significance of the predictors

found that large and animal-dispersed trees were less abundant near forest edges and gradually increased up to 100 m and more inside forest fragments.

Although the variability in species composition was correlated with the distance from the nearest forest edge (and fragment size), the observed differences between communities located at the edge and in the forest interior were gradual. Indeed, despite the high level of fragmentation in the studied landscape, we did not observe any homogenisation of tree communities near forest edges or in small fragments as suggested by Santos et al. (2008), Tabarelli et al. (2008) and Lôbo et al. (2011) in Brazil. Community changes rather followed different successional pathways depending on varying factors such as disturbance history and environmental variation, as well as neutral processes (see Ewers et al. 2017).

Lastly, edge-effects are definitely a critical issue for biodiversity conservation in the studied landscape. Indeed, as a result of fragmentation, today 75% of the remnant forest fragments are now 5 ha or less. Only seven out of the 52 sampled fragments contained

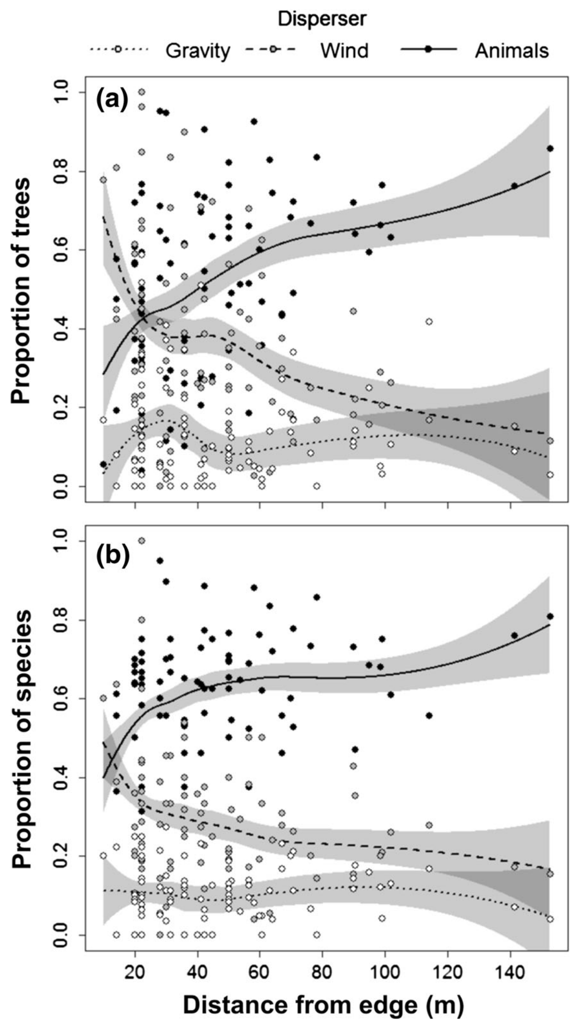


Fig. 5 Variability in the proportion of trees (**a**) and species (**b**) dispersed by gravity, wind or animals. *Lines* represent one standard deviation

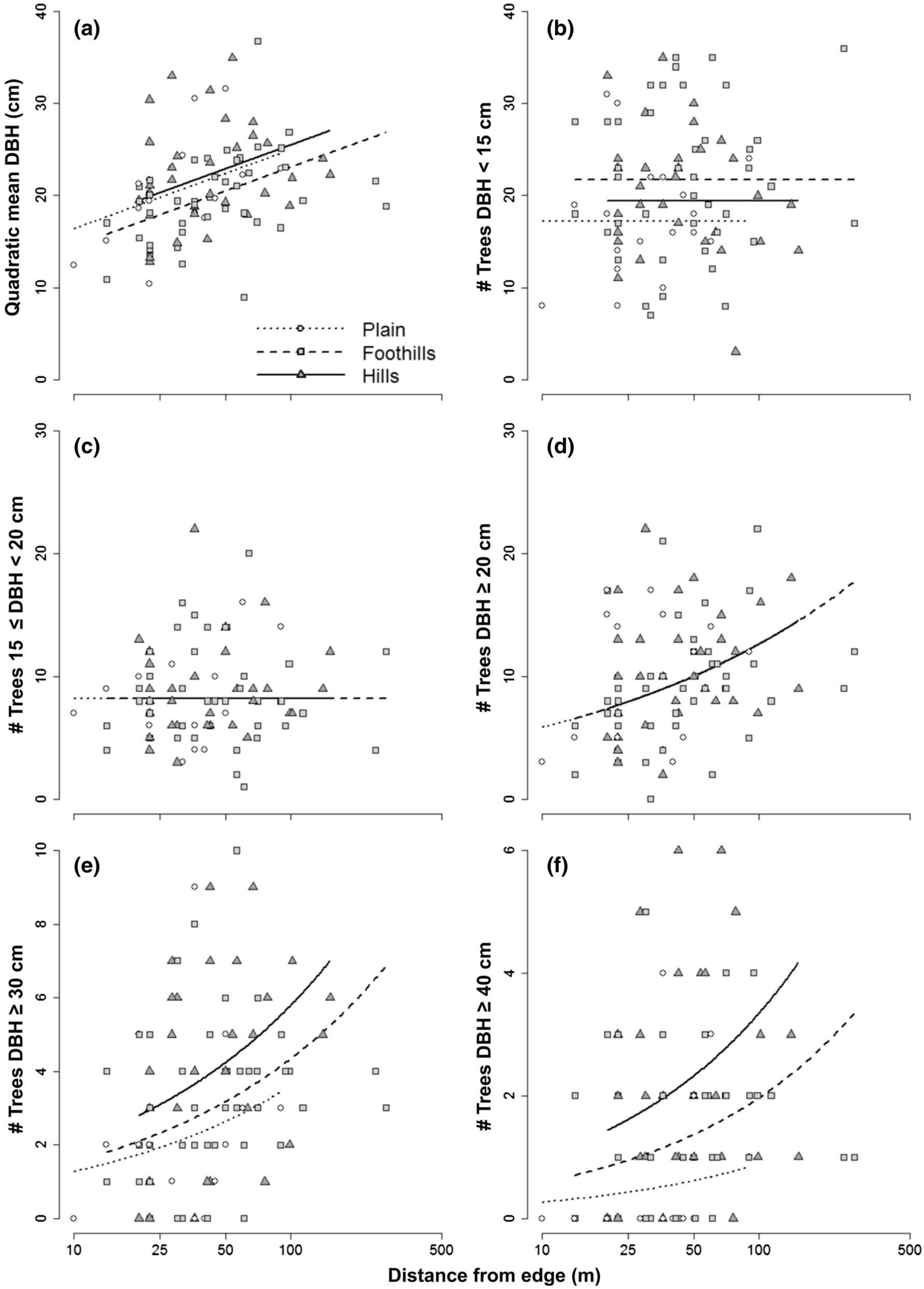
forest areas that were located further than 100 m from edges, and none of them further than 300 m. Such a high level of fragmentation is likely to promote major changes related to edge effects. Indeed, a decrease in fragment sizes increases the amount of forest area affected by edge-effects and the magnitude of changes in fragments with a small area or high perimeter-area ratio are amplified through multiple edge-effects (Malcolm 1994; Benitez-Malvido 1998; Fletcher 2005; Ewers and Laurance 2006; Laurance et al. 2006; Malcolm et al. 2017). Furthermore, a high fire frequency maintains strong contrasts between forest and the surrounding shrubby vegetation (McCoy et al. 1999; Perry and Enright 2002; Curt et al. 2015). These high contrasts are likely to further increase the strength and the depth of influence of edge-effects (Didham and Lawton 1999; Mesquita et al. 1999; Harper et al. 2005).

Effect of topography

Our results showed that the topographical position also significantly affects the structure and the composition of tree communities. Communities located on hills exhibited a greater abundance and richness of animal-dispersed trees and tended to have a higher density of large trees compared to communities located on foothills or in the plain. However, it is tricky to disentangle the effect of the environment from the effect of anthropogenic fragmentation, land use and disturbance level in shaping tree communities. Indeed, fragmentation is often a non-random process (Laurance 2008). In the studied area, logging and mining activities (including prospection), mainly affected forest on the foothills and on the flat area. Likewise, bushfires mainly propagated from the plain to the foothills and along the ridges, pushing back the forest into moist areas sheltered from wind (e.g. along talwegs, see Ibanez et al. 2013). As a result, the level of fragmentation, as well as the level of disturbance, was higher in the plain than on the hills. Also, the higher level of forest fragmentation in the plain may have resulted from the natural sparse distribution of suitable edaphic conditions for forest growth in the hydromorphic area. In addition, soil types, which are highly related to topography, are known to drive community structure and composition (Jaffré 1980; Jaffré and L'Huillier 2010a). Lastly, on the hills forest fragments were less exposed to wind and drought, which ought to have promoted the development and persistence of large late successional trees.

No effects of fragment size and isolation?

Finally, we did not detect any evidence of a fragment size or isolation effect on tree communities. Several issues may explain this result. First, the fragment size and edges have confounding effects (Ewers and Didham 2006; Fletcher et al. 2007; Banks-Leite et al. 2010; Didham et al. 2012). Indeed, as shown in our analysis, the size may affect tree communities through edge-effects; communities located in small fragment are more likely to be close to edges.



(a)
(b)
(c)
(d)
(e)
(f)
Quadratic mean DBH (cm)
Trees DBH < 15 cm
Trees 15 ≤ DBH < 20 cm
Trees DBH ≥ 20 cm
Trees DBH ≥ 30 cm
Trees DBH ≥ 40 cm
Plain
Foothills
Hills
10
25
50
100
500
Distance from edge (m)

◀**Fig. 6** Best models for the effect of the log-distance from the forest edge and the topographical position on the size of trees. Note that 15 and 20 cm correspond to the median and the third quartile of the DBH distribution, respectively. See Table 2 for the coefficients and significance of the predictors

Independently of edge-effects, the isolation of populations in small patches increases extinction probabilities (MacArthur and Wilson 1967). However, the processes leading to such extinction are usually long, notably for long-lived organisms such as trees. Like Metzger (2000) in Brazil, we suggest that the forest fragmentation found in the studied area is too recent (beginning at the end of the nineteenth century) relative to the long life-span of trees (centuries rather than decades) to already be able to observe changes in mature tree communities (DBH $\geq$ 10 cm) driven by the isolation of populations. Indeed, it has been shown that it can take centuries and even longer to fully pay the extinction debt due to population isolation (Helm et al. 2006; Vellend et al. 2006; Kolk and Naaf 2015). Alternatively, we suggest that we could not highlight any effect of fragment isolation because we did not take into account the heterogeneity of the matrix. Indeed, the nature of the matrix matters in the processes driving species assemblages in fragmented landscapes (see Kupfer et al. 2006; Laurance 2008). Notably, depending on its nature and its contrast with forest, the matrix may block, limit or facilitate the displacement of dispersers between forest fragments and even act as a habitat for forest species (Ricketts 2001; Murphy and Lovett-Doust 2004; Prevedello and Vieira 2010). It should be noted, however, that the integration of a heterogeneous matrix in the calculation of isolation or connectivity remains challenging because the effect of the matrix is highly species-dependent.

Conclusion

While most studies on the effect of tropical forest fragmentation on tree communities have been conducted in the neotropics, our study provides an original case study on a poorly known and highly threatened ecosystem. Disentangling the effects of the size and isolation of fragments from those of edges and fragment identity is challenging in landscape ecology. Here, after controlling for fragment identity, we found that after about a century of forest fragmentation edge-effects are likely to be the main processes that have affected remnant forest tree communities.

Our study calls for priority to be given to the conservation of large and compact forest fragments that are the more likely to maintain a forest core. Facing booming mining activities, most of the studied forest fragments are under the direct threat of land clearing in the near to medium term future. Forest fragmentation also needs to be stopped and forest extension promoted. Today, forest core is the only vegetation type protected by the environmental code; the surrounding vegetation including secondary forest at the edge and the vegetation matrix should also be protected to promote the long process of forest extension and subsequently reduce edge-effects. Forest extension should also be promoted by protecting forest edges and the surrounding vegetation against bushfires (e.g. by installing firebreaks).

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References

Alencar AA, Brando PM, Asner GP, Putz FE (2015) Landscape fragmentation, severe drought, and the new Amazon forest fire regime. Ecol Appl 25(6):1493–1505

Aubréville A, Leroy J-F, MacKee HS, Morat P (1967-present) Flore de la Nouvelle-Calédonie et Dépendances. Muséum National d'Histoire Naturelle, Paris

Banks-Leite C, Ewers RM, Metzger J-P (2010) Edge effects as the principal cause of area effects on birds in fragmented secondary forest. Oikos 119(6):918–926

Bartoń K (ed) (2016) {MuMIn}: multi-model inference, {R} package version 1.15.6

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67(1):48

Benchimol M, Peres CA (2015) Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. J Ecol 103(2):408–420

Benitez-Malvido J (1998) Impact of forest fragmentation on seedling abundance in a tropical rain forest. Conserv Biol 12(2):380–389

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. 24(3):127–135

Brando PM, Balch JK, Nepstad DC, Morton DC, Putz FE, Coe MT, Silvério D, Macedo MN, Davidson EA, Nóbrega CC, Alencar A, Soares-Filho BS (2014) Abrupt increases in Amazonian tree mortality due to drought–fire interactions. Proc Natl Acad Sci 111(17):6347–6352

Brinck K, Fischer R, Groeneveld J, Lehmann S, Dantas De Paula M, Pütz S, Sexton JO, Song D, Huth A (2017) High resolution analysis of tropical forest fragmentation and its impact on the global carbon cycle. Nat Commun 8:14855

Brooks RR (1987) Serpentine and its vegetation: a multidisciplinary approach. Dioscorides Press, Portland

Carpenter RJ, Read J, Jaffre T (2003) Reproductive traits of tropical rain-forest trees in New Caledonia. J Trop Ecol 19:351–365

Curt T, Borgniet L, Ibanez T, Moron V, Hély C (2015) Understanding fire patterns and fire drivers for setting a sustainable management policy of the New-Caledonian biodiversity hotspot. For Ecol Manage 337:48–60

Demenois J, Ibanez T, Read J, Carriconde F (2017) Comparison of two monodominant species in New Caledonia: floristic diversity and ecological strategies of *Arillastrum gummiferum* (Myrtaceae) and *Nothofagus aequilateralis* (Nothofagaceae) rainforests. Aust J Bot 65(1):11–21

Didham RK, Kapos V, Ewers RM (2012) Rethinking the conceptual foundations of habitat fragmentation research. Oikos 121(2):161–170

Didham RK, Lawton JH (1999) Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica 31(1):17–30

Dorner B, Lertzman K, Fall J (2002) Landscape pattern in topographically complex landscapes: issues and techniques for analysis. Landscape Ecol 17(8):729–743

Ewers RM, Andrade A, Laurance SG, Camargo JL, Lovejoy TE, Laurance WF (2017) Predicted trajectories of tree community change in Amazonian rainforest fragments. Ecography 40(1):26–35

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81(1):117–142

Ewers RM, Laurance WF (2006) Scale-dependent patterns of deforestation in the Brazilian Amazon. Environ Conserv 33(3):203–211

Ewers RM, Thorpe S, Didham RK (2007) Synergistic interactionsbetween edge and areaeffects in a heavily fragmented landscape. Ecology 88(1):96–106

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. J Biogeogr 40(9):1649–1663

Fletcher RJ (2005) Multiple edge effects and their implications in fragmented landscapes. J Anim Ecol 74(2):342–352

Fletcher RJ, Ries L, Battin J, Chalfoun AD (2007) The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? Can J Zool 85(10):1017–1030

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM, Damschen EI, Ewers RM, Foster BL, Jenkins CN, King AJ, Laurance WF, Levey DJ, Margules CR, Melbourne BA, Nicholls AO, Orrock JL, Song D-X, Townshend JR (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1(2)

Harper KA, Macdonald SE, Burton PJ, Chen JQ, Brosofske KD, Saunders SC, Euskirchen ES, Roberts D, Jaiteh MS, Esseen PA (2005) Edge influence on forest structure and composition in fragmented landscapes. Conserv Biol 19(3):768–782

Helm A, Hanski I, Partel M (2006) Slow response of plant species richness to habitat loss and fragmentation. Ecol Lett 9(1):72–77

Ibanez T, Birnbaum P (2014) Monodominance at the rainforest edge: case study of Codia mackeeana (Cunoniaceae) in New Caledonia. Aust J Bot 62(4):312–321

Ibanez T, Borgniet L, Mangeas M, Gaucherel C, Géraux H, Hély C (2013) Rainforest and savanna landscape dynamics in New Caledonia: towards a mosaic of stable rainforest and savanna states? Austral Ecol 38(1):33–45

Isnard S, L'Huillier L, Rigault F, Jaffre T (2016) How did the ultramafic soils shape the flora of the New Caledonian hotspot? Plant Soil 403(1–2):53–76

Jaffré T (1980) Etude écologique du peuplement végétal des sols dérivés de roches ultrabasiques en Nouvelle-Calédonie. Paris Sud-Orsay

Jaffré T, Bouchet P, Veillon JM (1998) Threatened plants of New Caledonia: is the system of protected areas adequate? Biodivers Conserv 7(1):109–135

Jaffré T, L'Huillier L (2010a) Conditions de milieu des terrains miniers. In: L'Huillier L, Jaffré T, Wulff A (eds) Mines et environement en Nouvelle-Calédonie: les milieux sur substrats ultramafiques et leur restauration. IAC, Nouméa, pp 33–44

Jaffré T, L'Huillier L (2010b) La végétation des roches ultramafiques ou terrains minier. In: L'Huillier L, Jaffré T, Wulff A (eds) Mines et environnement en Nouvelle-Calédonie: les milieux et substrats ultramafiques et leur restauration. IAC, Nouméa, pp 45–103

Jaffré T, Rigault F, Dagostini G, Tinel-Fambart J, Wulff A, Munzinger J (2009) Input of the different vegetation units to the richness and endemicity of the New Caledonian flora. In: Pacific science intercongress, Tahiti

Jesus FM, Pivello VR, Meirelles ST, Franco G, Metzger JP (2012) The importance of landscape structure for seed dispersal in rain forest fragments. J Veg Sci 23(6):1126–1136

Kazakou E, Dimitrakopoulos PG, Baker AJM, Reeves RD, Troumbis AY (2008) Hypotheses, mechanisms and trade-offs of tolerance and adaptation to serpentine soils: from species to ecosystem level. Biol Rev 83(4):495–508

Kolk J, Naaf T (2015) Herb layer extinction debt in highly fragmented temperate forests - Completely paid after 160 years? Biol Conserv 182:164–172

Kupfer JA, Malanson GP, Franklin SB (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. Glob Ecol Biogeogr 15(1):8–20

Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Ockinger E, Partel M, Pino J, Roda F, Stefanescu C, Teder T, Zobel M, Steffan-Dewenter I (2009) Extinction debt: a challenge for biodiversity conservation. Trends Ecol Evol 24(10):564–571

Laurance WF (2008) Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. Biol Conserv 141(7):1731–1744

Laurance WF, Delamonica P, Laurance SG, Vasconcelos HL, Lovejoy TE (2000) Conservation: rainforest fragmentation kills big trees. Nature 404(6780):836

Laurance WF, Nascimento HEM, Laurance SG, Andrade AC, Fearnside PM, Ribeiro JEL, Capretz RL (2006) Rain forest fragmentation and the proliferation of successional trees. Ecology 87(2):469–482

L'Huillier L, Jaffré T (2010) L'exploitation des minerais de nickel en Nouvelle-Calédonie. In: L'Huillier L, Jaffré T, Wulff A (eds) Mines et environement en Nouvelle-Calédonie: les milieux sur substrats ultramafiques et leur restauration. IAC, Nouméa, pp 21–31

Lôbo D, Leão T, Melo FPL, Santos AMM, Tabarelli M (2011) Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. Divers Distrib 17(2):287–296

MacArthur RH, Wilson EO (1967) The theory of island biogeograpy. Princeton University Press, Princeton

Magnago LFS, Edwards DP, Edwards FA, Magrach A, Martins SV, Laurance WF (2014) Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. J Ecol 102(2):475–485

Malcolm JR (1994) Edge effects in central Amazonian forest fragments. Ecology 75(8):2438–2445

Malcolm JR, Valenta K, Lehman SM (2017) Edge effects in tropical dry forests of Madagascar: additivity or synergy? Landscape Ecol 32(2):327–341

McCoy S, Jaffré T, Rigault F, Ash JE (1999) Fire and succession in the ultramafic maquis of New Caledonia. J Biogeogr 26(3):579–594

Mendes G, Arroyo-Rodríguez V, Almeida WR, Pinto SRR, Pillar VD, Tabarelli M (2016) Plant trait distribution and the spatial reorganization of tree assemblages in a fragmented tropical forest landscape. Plant Ecol 217(1):31–42

Mesquita RCG, Delamônica P, Laurance WF (1999) Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. Biol Conserv 91(2–3):129–134

Metzger JP (2000) Tree functional group richness and landscape structure in a Brazilian tropical fragmented landscape. Ecol Appl 10(4):1147–1161

Mittermeier RA, Robles Gil P, Hoffmann M, Pilgrim J, Brooks T, Mittermeier CG, Lamoureux J, da Fonseca GAB (2004) Hotspots Revisted. Chicago University Press, Chicago

Morat P, Jaffre T, Tronchet F, Munzinger J, Pillon Y, Veillon JM, Chalopin M, Birnbaum P, Rigault F, Dagostini G, Tinel J, Li PP (2012) The taxonomic reference base "Florical" and characteristics of the native vascular flora of New Caledonia. Adansonia 34(2):179–221

Murcia C (1995) Edge effects in fragmented forests—implications for consevation. Trends Ecol Evol 10(2):58–62

Murphy HT, Lovett-Doust J (2004) Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? Oikos 105(1):3–14

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol Evol 4(2):133–142

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2013) vegan: Community Ecology Package

Oliveira MA, Santos AMM, Tabarelli M (2008) Profound impoverishment of the large-tree stand in a hyper-fragmented landscape of the Atlantic forest. For Ecol Manage 256(11):1910–1917

Orihuela RLL, Peres CA, Mendes G, Jarenkow JA, Tabarelli M (2015) Markedly divergent tree assemblage responses to tropical forest loss and fragmentation across a strong seasonality gradient. PLoS ONE 10(8):e0136018

Pascal M, Richer de Forges BR, Le Guyader H, Simberloff D (2008) Mining and other threats to the New Caledonia biodiversity hotspot. Conserv Biol 22(2):498–499

Perry GLW, Enright NJ (2002) Humans, fire and landscape pattern: understanding a maquis-forest complex, Mont Do, New Caledonia, using a spatial 'state-and-transition' model. J Biogeogr 29(9):1143–1158

Prevedello JA, Vieira MV (2010) Does the type of matrix matter? A quantitative review of the evidence. Biodivers Conserv 19(5):1205–1223

Proctor J, Lee YF, Langley AM, Munro WRC, Nelson T (1988) Ecological studies on Gunung Silam, a small ultrabasic mountain in Sagah, Malaysia. I. Environements, forest structure and floristics. J Ecol 76(2):320–340

Richer de Forges B, Pascal M (2008) La Nouvelle-Calédonie, un "point chaud" de la biodiversité mondiale gravement menacé par l'exploitation minière. J de la Société des Océanistes 126–127:95–112

Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. Am Nat 158(1):87–99

Santos BA, Peres CA, Oliveira MA, Grillo A, Alves-Costa CP, Tabarelli M (2008) Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. Biol Conserv 141(1):249–260

Tabarelli M, Lopes AV, Peres CA (2008) Edge-effects drive tropical forest fragments towards an early-successional system. Biotropica 40(6):657–661

Team RC (2012) R: a language and environment for statistical computing, 2.15.2 edn, Vienna, Austria

Turner MG (1989) Landscape ecology: the effect of pattern and process. Annu Rev Ecol Syst 20:171–197

Turner IM (1996) Species loss in fragments of tropical rain forest: a review of the evidence. J Appl Ecol 33(2):200–209

van der Ent A, Jaffre T, L'Huillier L, Gibson N, Reeves RD (2015) The flora of ultramafic soils in the Australia-Pacific Region: state of knowledge and research priorities. Aust J Bot 63(3–4):173–190

Vellend M, Verheyen K, Jacquemyn H, Kolb A, Van Calster H, Peterken G, Hermy M (2006) Extinction debt of forest plants persists for more than a century following habitat fragmentation. Ecology 87(3):542–548

Wilcove DS, McLellan CH, Dobson AP (1986) Habitat fragmentation in the temperate zone. In: Soule ME (ed) Conservation biology. The Science of Scarcity and Diversity, Sinauer, pp 237–256

Wilson MC, Chen X-Y, Corlett RT, Didham RK, Ding P, Holt RD, Holyoak M, Hu G, Hughes AC, Jiang L, Laurance WF, Liu J, Pimm SL, Robinson SK, Russo SE, Si X, Wilcove DS, Wu J, Yu M (2016) Habitat fragmentation and biodiversity conservation: key findings and future challenges. Landscape Ecol 31(2):219–227